New perspectives on taste and primate evolution: the dichotomy in gustatory coding for perception of beneficent vs. noxious substances as supported by correlations among human thresholds

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(Version 35. October 2000. Submitted to: American Journal of Physical Anthropology)

New perspectives on taste and primate evolution: the dichotomy in gustatory coding for perception of beneficent vs. noxious substances as supported by correlations among human thresholds

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Key words selective pressure; taste perception; sugars; tannins; alkaloids; sodium chloride; food aversions

Abstract In various environments where primates are presently observed, as well as in forests and savannas which have been inhabited by australopithecines and early hominids, there are –or there has been presumably– categories of substances eliciting taste signals associated with stereotyped responses. Such is the case for various soluble sugars of fruits and nectars, attracting consumers; and for several plant compounds in which bitter or strongly astringent properties have a repulsive effect. The occurrence of such classes of tasty substances among natural products appears to be related to the evolutionary trends that shaped primate sensory perception (for detecting either beneficent or potentially noxious substances) in the context of a long history of coevolution between animals and plants. In this paper, we present original psychophysical data on humans (412 individuals aged 17 to 59 years) as an analogy with which to test recent evidence from electrophysiology in nonhuman primates (Hellekant et al., [1997] J. Neurophysiol. 77:978-993; Danilova et al., [1998] Ann. NY Acad. Sci. 855:160-164) that taste fibers can be grouped into clusters of "best responding fibers" with two more specific clusters, one for sugars and one for quinine and tannins. The collinearity found between human taste responses (recognition thresholds) for fructose and sucrose, as well as for quinine and tannins, is presented and discussed as another evidence of the two-direction evolutionary trends determining taste sensitivity. Salt perception appears to be totally independent of these trends. Accordingly, the appreciation of a salty taste seems to be a recent culturally learned response, not a primary taste perception. The very existence of primary tastes is discussed in the context of evolutionary trends, past and present. Am J Phys Anthropol .....

Taste perception is generally considered to be an adaptive response for assessing nutritional content (Le Magnen, 1985) and/or coping with toxicity in potential foods through the recognition of a few basic or "primary tastes" (including sweet, bitter, salty, sour, umami, and possibly other tastes). However, the evolutionary scenarios relating "primary taste qualities" to corresponding chemical stimuli are not wholly convincing.

Strong evidence exists that fleshy fruits containing sugars coevolved with taste perception in fruit eaters (most primates are frugivorous), allowing simultaneous seed dispersal of the phanerogams (the flowering plants that evolved after the Mesozoic) and the meeting of the energy requirements of fruit consumers: the larger the animal, the lower the perception threshold for sugar (Simmen and Hladik, 1998). There is also evidence that "secondary compounds" retained by plants to reduce damage by plant eaters (Rosenthal and Janzen, 1979) resulted in coevolution of taste perception. Avoidance of toxic substances (such as alkaloids) through the detection of a bitter taste (as perceived by humans) varies among primate species in relation to the potential toxicity of plants in various environments (Simmen, 1994). However a large number of bitter tasting substances are not toxic, and the cost/benefit ratio of evolving sensitivity to bitterness would not be advantageous to several species of plant eaters (Glendinning, 1994).

Salt perception appears even more puzzling in the context of coevolution. Most researchers evoque the importance of sodium in animal physiology and its relative rarity in most environments to explain the emergence of a salty taste response, without taking into account the fact that sodium nutritional needs are largely covered by most natural diets, especially in primates for whom the range of the perception threshold for sodium chloride does not allow to taste the concentrations found in most vegetables they eat (Hladik and Simmen, 1996). Since salt was used, and often added to human food, during a relatively recent period of primate evolution, can we actually talk about the evolution of a salty taste response? Similarly, the intuition that other "basic tastes" such as sour and umami (the taste of monosodium glutamate), evolved by virtue of the fact that they contributed to the avoidance of acidity and the detection of nitrogen-rich foods, would require more evidence.

Whatever adaptive pressures actually determined taste responses, the evolution of taste perception, based on the transduction of chemical stimuli into electrophysiological signals, must be reflected in the presence of genes coding either for peripheral specific taste receptors, or for brain structures allowing central information processing, or for both (Erickson, 1963, Pfaffmann et al., 1971). As far as the peripheral taste system is concerned, two theories are currently proposed that partly reflect a dilemma surrounding the "basic tastes". Whereas the "across-fiber pattern theory" assumes that every taste stimulus will elicit a response in every taste fiber (Erickson et al., 1965), the "labeled-line theory" suggest that a taste quality could be linked exclusively to the activity found in a particular taste fiber, as

discussed by Smith and Frank (1993).

Recent electrophysiological/behavioral investigations on primates by Hellekant and Ninomiya (1994), Hellekant et al. (1997a, 1998) and Danilova et al. (1998) have made significant contributions to the debate on taste coding. By recording impulses on isolated taste fibers during stimulation of the tongue by various solutions (including sugars, alkaloids, salts and acids), these authors showed that fibers can be grouped into clusters of "best responding fibers" although they generally respond to several stimuli. The most specific cluster was found with sugars and other sweet substances (as perceived by humans). A second cluster was also clearly demonstrated with fibers responding mostly to alkaloids (quinine, caffeine) and polyphenols such as tannic acid, all substances for which tasting induces immediate rejection in behavioral tests. Other clusters of "best responding fibers" (for salt and acid) have been identified, but they include fibers also responding to various other substances; and these clusters vary among primates.

Such properties of peripheral taste fibers can result from selective pressures within a two-directional system (nutrient content vs toxicity). Only two sets of electrophysiological/behavioral entities (instead of four or more discrete basic entities) of taste fibers/responses have been clearly observed among primates and some other mammals, corresponding, in terms of behavior, respectively to acceptance (for sugars) and rejection (for alkaloids and polyphenols).

Could the electrophysiological evidence of such taste fiber properties in primates be tested in humans, using psychophysical data in the analogy? We addressed this issue by considering the collinearity between taste thresholds for different substances as related to the occurrence of "best responding fibers" for each tasting substance, and to the corresponding information conveyed by the taste fibers of different sets.

In this paper, we will frame our discussions within a primatological/ anthropological viewpoint, placing our data on human taste responses in an evolutionary perspective.

Subjects and Methods

Our data concern a sample of 412 individuals of both sexes (131 men, 281 women, aged 18 to 59 years [mean: 36.0, SD: 10.7]) tested during different cross-cultural studies (Gerber and Padilla, 1998; Malet et al., 1999a; Simmen et al., 1999; Pasquet and Oberti, 2000; Iaconelli, 2000) in the European Union, Russia, Tunisia, and Cameroon. The initial purpose of these studies was to investigate variation of taste sensitivity in different populations/environments previously observed by one of us (Hladik et al., 1986). To minimize the possible effect of aging on taste perception (Bourlière et al., 1958; Bartoshuk et al., 1986) all subjects over 60 years old have been excluded from our working sample.

After informing the subject on taste categories he or she could be presented with (water, salty, sour, sweet, bitter and astringent), thresholds were determined by presenting, in a semi-randomized order (blind test), various of solutions of purified products, starting with the weakest solution in order of increasing concentration (0.3 log steps), until recognition. Solutions were presented in a 2 ml plastic teaspoon and were expectorated by the subject after tasting. Once the subject commented on the taste he rinsed his mouth and one minute elapsed before the next assay. After the subject first recognized the taste of a solution, concentrations above and below preliminary estimated threshold level were presented, again until unambiguous recognition.

Solutions of sucrose (1.5-1600 mM), fructose (2-1000 mM), sodium chloride (4-1000 mM), quinine hydrochloride (0.8-400 μM), citric acid (0.2-25 mM), tannic acid (4-4000 μM) and oak tannin (0.03-8 g/l; OEnofrance; undetermined molecular weight) were presented. Sensitivity to 6-n-propylthiouracyl (PROP) was also investigated after testing the previous substances, using a simplified method with two solutions to determine the taster/non-taster status of a subject. Tasters recognize a bitter taste at 0.1 mM and non-tasters at or above 0.2 mM (Bartoshuk, 1979); however, a full range of 13 PROP solutions (0.001-3.8 mM) was used in the Tunisian sample (N=118) to cross-validate, in our data, the two-solution method. Since "water" was among the possible tastes to be named, local drinking water was used to prepare the solutions and for rinsing the mouth between tests.

Probit analysis (Finney, 1971) was carried out to estimate mean recognition thresholds using the probit procedure of the SAS package (SAS Institute, 1994). Hierarchical cluster analysis was performed using the statistical package SYSTAT version 9.0 (SPSS Inc., Chicago). Intercluster similarity was measured using the Pearson correlation coefficient, and cluster analysis processed according to the average linkage method (Sneath and Sokal, 1973). Missing values (including unclear responses, eliminated from our working sample) were handled using the expectation-maximization method (Little, 1988). This procedure defines a model for the partially missing data and bases inferences on the maximum likelihood method. Underlying distributions for the PROP thresholds, and the concentration cutoff point for non-tasting, were determined in the Tunisian sample using maximum likelihood following the SKUMIX program (McLean et al., 1976).

Results

Results of the probit analysis for the recognition thresholds of different substances are presented in Table 1. No significant correlation was found between age and taste threshold for all tested substances, neither for men nor for women.

No departure from the probit model was observed in the data: the Chi square values of the goodness of fit are small for all analyses ($p<0.001$), suggesting that recognition thresholds are normally distributed. The mean recognition thresholds

for sucrose, fructose, sodium chloride, quinine hydrochloride and citric acid, all fall within the range of the values observed in humans by Hladik et al. (1986), using a similar blind procedure. Our working sample includes 21.5 % of PROP non-tasters, the local variations in sub-samples falling in the range of published observations for PROP and analogs (Hladik and Pasquet, 1999). The SKUMIX procedure applied to the Tunisian sample yielded a distribution of PROP thresholds which is more likely bimodal than mono-modal (Chi^2= 21.2; p< 0.001). The estimated antimode concentration is 0.24 mM, thus validating the use of the concentration 0.2 mM to discriminate tasters vs. non tasters with the two-solution method.

Correlations between thresholds (Table 2) provide the highest linkages among sugars as well as among tannins (r=0.51 and 0.50 respectively). Most remarkable are the significant correlations between quinine hydrochloride and the tannins(r=0.32 and 0.39), that is, for each individual, the higher quinine taste threshold, the higher tannin taste thresholds. The sodium chloride threshold is not specifically linked to any of the other compounds tested, and no noticeable correlation was found between the PROP status and the sensitivity to any other substance.

Figure 1 is the cluster tree illustrating the collinearities between the taste responses. We notice that tasting sugars, as well as tannins, cluster separately at the shortest distances (1-r=0.51 and 0.44 respectively). Tasting of tannins aggregate with tasting of quinine hydrochloride into another cluster (1-r=0.60). Tasting of citric acid and of sodium chloride do not cluster clearly with the other substances, but present a weak collinearity (1-r=0.79) with the quinine/tannins cluster.

Segregating data according to sex categories did not reveal any departure from the above cluster tree. Similarly, when considering separately the population sub-sample with the most complete data fields (Tunisian, N=118), the shape of the cluster tree does not differ from Figure 1. This model thus appears to be a robust one.

Discussion

From the perspective of evolutionary anthropology, the aim of our study was to determine the relationships among human taste thresholds in an attempt to make analogical comparisons with the clusters of “best responding taste fibers” observed in nonhuman primates by Hellekant and Danilova (1996). Methods used with humans necessarily differ from those used with nonhuman primates for which the determination of taste thresholds may require several months using the two-bottle test in an animal house (Simmen and Hladik, 1988). In contrast, an anthropologist can conduct several tests in half an hour with the cooperation of the tested person, allowing taste profile comparisons to be made on a large number of individuals in a relatively short time. Both methods aim at determining a functional response (recognition threshold), allowing the actual discrimination of a compound in foodstuffs to be made.

As demonstrated by the analysis of our data, collinearity between human taste thresholds applies to two groups of natural compounds of major significance in terms of feeding ecology: sugars (providing energy) and quinine/tannins, the most abundant plant "secondary compounds" (generally toxic). The clear dichotomy between these two groups in the cluster tree (Fig. 1) illustrates the contrast between the two sets of tastes (generally perceived as pleasant vs. unpleasant). Proximity within the sugar group and within the group of quinine and tannins is likely to reflect, in each group, a partly similar taste perception corresponding to partly similar peripheral signals.

Electrophysiological records in primates show that two main clusters of taste peripheral single fibers are common to all species tested so far (chimpanzee, macaque, marmoset): on the one hand, taste fibers responding preferentially to sugars and other sweet substances; on the other hand, taste fibers responding preferentially to quinine and several substances tasting bitter to humans, as well as to tannins (Hellekant and Ninomiya, 1994; Hellekant et al., 1997b, 1998; Danilova et al., 1998). Other clusters observed (for instance for various salts and/or acids) are not shared by all primate species.

Taking into account the converging aspects of the results of these investigations, we can hypothesize that two major sets of selective pressures have, throughout evolutionary history, shaped the gustatory system of primates, including that of australopithecines and early hominids. These pressures are the need for beneficent compounds and the necessity to avoid toxic substances. Genes determining gustatory abilities are obviously the target of selective pressures. Although we are not focusing the present study on taste genetics, some genetic evidence needs to be presented, together with functional aspects of the taste system.

Taste perception of beneficent substances

The radiation of Primates took place during the diversification of Angiosperms, which occurred between some 135 million years ago and now. Thus, the ability to taste sweet compounds in this Order has evolved in parallel with the rise of plants bearing flowers and fleshy fruits (Hladik, 1993).

It is remarkable that despite specific morphological features allowing primates to cope with different food types all primates tested to date display a marked preference for sugars, with species differing in taste thresholds (Glaser, 1986; Simmen, 1994). One can hypothesize that the taste system evolved in connection with the digestive tract to permit food choices to adjust to resources that species are able to process. In this respect, one might wonder whether taste responses at a peripheral level are not basically a reflection of what should be immediately perceived as edible or inedible, given species digestive abilities.

The gusto-facial reflex has been presented as an “innate” response to gustatory stimuli (Steiner, 1977). When applied on the tongue of adult or juvenile primates, a

sucrose solution invariably leads to a relaxed expression of the face associated with sucking and licking movements (Steiner and Glaser, 1984). This was demonstrated in various primate species including human babies of less than one-day old. Environmental modulation of this reflex may occur at an intrauterine stage or following birth, but the fact that the stereotyped expression of the face is also found in anencephalous newborns who only possess brain stem and mesencephalon (thus being deprived of associative areas), argues for a genetic origin. It should be noted that such a reflex is not linked to the hedonic character of sweet taste perception which involves mobilization of higher brain structures.

The moderate aggregation distance (0.51) in the sucrose/fructose cluster shown in Figure 1, as well as in peripheral taste fiber cluster found in nonhuman primates by Hellekant et al. (1997b, 1998) for sugars and other substances tasting sweet (to humans), suggest that the gusto-facial reflex is not triggered by a single signal (i.e. a basic sweet taste quality). The genes coding for this innate function of the taste system would be multiple, as indicated by the fact that different sugars elicit partly distinct peripheral signals, as shown by Faurion et al. (1980) and Faurion and Mac Leod (1982).

Although data on the genetics of sugar perception in primates are lacking, a twin study in humans (Krondl et al., 1983) yielded an heritability index of 0.52 for the sucrose recognition threshold, approaching but not achieving statistical significance. Models for other mammals have been developed (Lush, 1989). Recent evidence has been found that genes determine peripheral sucrose sensitivity in mice, with one locus affecting the response threshold and another locus the response magnitude (Bachmanov et al., 1997).

Taste thresholds for sugars, evolved in different primate species, allow various feeding strategies to develop. A low taste threshold for sugars (i.e. high sensitivity) not only permits the seeking of high calorie foods, but also the utilization of a wide range of food items having a low sugar content yet perceived as edible. Conversely a high threshold for sugars corresponds to a feeding strategy limited to high energy foods. The differentiation into these two contrasted strategies has been inferred from the allometric relationship between taste threshold and body weight: the larger the primate, the higher the energy need (Simmen and Hladik, 1998). This is a global tendency, however; sugar sensitivity can diverge from this trend among species of similar size living in different environments, especially when rain forests are compared with open environments (the latter harboring plants bearing fruits with a low sugar content). The significant difference in taste threshold for sucrose observed in human groups living at a subsistence level in these two contrasted environments has been interpreted as a result of environmental selective pressures (Hladik and Simmen, 1993).

At this point, it is worth mentioning the discovery of a discontinuity among primates in the perception of natural compounds (such as the proteins thaumatin and monellin) that humans consider sweet. These compounds, among which are

some that appear 100,000 times as sweet as sucrose to humans, elicit a response on the peripheral taste nerve in Catarrhine monkeys, but are not perceived by Platyrrhines and most prosimians (Glaser et al., 1978). Accordingly, receptor sites evolved independently from the common ancestor of Old World and New World monkeys, allowing only in one case the fortuitous binding with the sweet proteins evolved in plant species "mimicking" the taste of sugar perceived by African primates (Hladik, 1993). Although separated 30 million years ago and having distinct taste receptors, these groups of primate species, as well as prosimians, remain able to taste soluble sugars, a character that has certainly been a target for selective pressures, given the importance of sugars as sources of readily assimilable energy.

In addition, when comparing responses of isolated taste fibers of Chimpanzee, Macaques and two other mammals (hamster and pig), Hellekant and Danilova (1996) showed that all compounds that taste sweet to human elicit responses from a group of "best responding fibers" in chimpanzee. However the effect of different sweeteners on primate taste fibers vary; and other mammals not necessarily respond to all sweeteners. The similarity of taste responses in man and chimpanzee parallels the genetic proximity of these two species evolved in Africa.

Taste responses to several other substances necessary to a balanced diet have been considered as adaptive. For instance, sensitivity to sodium chloride would have evolved in response to the necessity of maintaining the osmotic body balance. The apparently universal acceptance of salty foods by 4-6 month old human infants would have an "unlearned", possibly genetic, basis (Beauchamp and Cowart., 1985; Mela and Catt, 1997). However, the adaptive interpretation seems highly questionable from the evidence in non-primates: the range of thresholds for sodium chloride found in most species is above the actual content in natural foodstuffs (generally below 0.5% of the dry weight, i.e. less than 20 mM; Hladik and Simmen, 1996). An efficient adaptation would have resulted in lower thresholds, allowing recognition of the sodium content of available foods.

In the same vein, the "umami taste" of monosodium glutamate would be adaptive to nitrogen and amino acid balance (Kawamura and Kare, 1987). The discovery in the primate chorda tympani nerve of single fibers responding preferentially to monosodium glutamate (MSG) by Hellekant et al. (1997a) and the apparently unique taste quality of this compound led to the hypothesis that the umami taste may have evolved as a signal of protein occurrence in foods.

Amino acids are usually tasted differently according to their L- or D-enantiomers in humans as well as in nonhuman primates (Haefeli and Glaser, 1990). Actually, L-amino acids, which are the naturally occurring forms, are more frequently described as bitter or repulsive by human subjects. Preference tests in nonhuman primates show that the L-amino acids are attractive, unlike several D-forms (Glaser, 1986). These results may simply be explained by the fact that free soluble amino acids are rare in plants selected by primates; they occur as small peptides that are probably not detected by taste. Following the biochemical analysis

of natural fruits and leaves selected by plathyrrhine primates, Simmen and Sabatier (1996) found that the contents of amino acids present in the soluble fraction of foods were lower than 1.4% by dry weight (around 0.01 mM in the juice) whereas thresholds for tryptophan are above 0.1 mM (Glaser, 1986).

Actually, salts and amino acids —essential elements in the diet— appear to determine feeding choices through mechanisms independent of the immediate taste perception. Such mechanisms involve, for all mammals, a sensory reward associated with the long-term beneficent effect of satiety (Le Magnen, 1985). The perception of food items as beneficent may thus result from conditioned preferences for tastes (or flavors) other than those of the essential elements per se (Toates, 1986).

Adaptive trends and the taste of noxious substances

Food avoidance can also result from a conditioned taste aversion in which the taste actually perceived is not that of the noxious element. Garcia and Koelling (1966) showed the great efficiency of this type of conditioning, aversion being acquired immediately after the first trial.

Nevertheless unlearned gusto-facial responses to quinine, consisting of an arch-shaped contracted mouth and protruded tongue, have been clearly observed in human and nonhuman neonates (Steiner and Glaser, 1984). The adaptive value of this reflex, which allows a potentially toxic substance to be spat out, is obvious. Alkaloids (such as quinine), which often taste bitter to humans, and polyphenols (such as tannins), which are strongly astringent, occur frequently in primate environments. Such an abundance of "secondary compounds" probably resulted from interactions between consumers and plants (Rosenthal and Janzen, 1979), a coevolution starting long before primates occupied the various feeding niches.

Primate taste thresholds for quinine hydrochloride vary largely (0.0006 - 0.8 mM) among species (Simmen et al., 1999a). The lowest threshold (high sensitivity) was observed in Callithrix argentata, a species inhabiting a peculiar forest environment where "secondary compounds" are likely to be highly toxic. In contrast, a closely related species (Cebuella pygmaea) living in a rain forest where alkaloids are not likely to be toxic, has a 1,000-fold higher threshold (Simmen, 1994). Did the relatively low human threshold at 0.012 mM (Table 1) result from the toxicity of the plants that early hominids had to cope with (Johns, 1990)?

In human populations, as well as in mice, the distribution of quinine sensitivity shows a polygenic determination (Fisher and Griffin, 1963; Smith and Davies, 1973; Lush, 1984; Whitney and Harder, 1994). Polymorphism of taste responses with other bitter tasting compounds such as phenylthiocarbamide (PTC) and its chemical relative, 6-n-propylthiouracyl (PROP), indicates a determination by no more than one or two genes in man (Blakeslee, 1932; Olson et al., 1989). This peculiar genetically determined taste perception was also found in mice and nonhuman primates (Klein and DeFries, 1970; Harder and Whitney, 1998; Eaton and Gavan,

1965).

Since we did not find co-variation of quinine threshold and PROP taster status in man (Fig. 1), primate taste evolution could have been exclusively determined by the naturally occurring toxic chemicals (alkaloids, such as quinine). Several kinds of "bitter tastes" (as perceived by humans) correspond to various systems of peripheral stimulation (Kurihara et al., 1994) and probably to several genes. The bitter perception of artificial chemicals such as PROP could be fortuitous; and its oversimplified genetic determination, may imply a small part (or just one) of the multiple taste receptors stimulated by other bitter substances.

In contrast, co-variation of thresholds for quinine and tannins is clearly established by our cluster analysis (Fig. 1). Similarly, Danilova et al. (1998) observed that the same isolated taste fiber of a nonhuman primate responds to quinine, caffeine and tannic acid.

Taste perception of tannins has been recently investigated in primates (Simmen et al., 1999a; Iaconelli, 2000), but little is known about the threshold variation among species. The figures for oak tannin and tannic acid have never been determined on large samples of human populations. However, it is noticeable that responses recorded by Hellekant et al. (1993) on the chorda tympani of the primate Microcebus murinus after tongue stimulation with tannic acid, show that the perception threshold falls within the same range (0.075-0.2 mM) as that of human populations tested (Table 1). Behavioral tests on the same prosimian species show that the inhibition threshold for mixtures of fructose/tannin are around 0.11-0.44 mM tannic acid (Simmen et al., 1999b; Iaconelli and Simmen, 1999).

The present lack of investigation on tannin taste is surprising given the generalized occurrence of tannins and other polyphenols in primate natural diet, and, most likely, in the diet of autralopithecines and early hominids (Johns, 1990; Simmen et al., 1999a). It must be, at least in part, due to the predominance, during half a century, of the "basic tastes" theory (McBurney and Gent, 1979). Astringency (or references to other terms related to tannin perception) was not considered to be a basic taste, but a tactile sensation (Breslin et al., 1993). Indeed, several tannins elicit a sensation of "dryness" in the oral cavity because they bind strongly to salivary proteins (this binding property of tannins has been used for centuries to convert raw hide into leather). But, besides the tactile sensation, there is evidence for the simultaneous transmission of other information on taste nerve fibers after stimulating the tongue with various tannins (Hellekant et al., 1993; Danilova et al., 1998). For humans, biting an immature fruit with a high tannin content —such as persimmon (Diospyros kaki), or blackthorn (the doe, Prunus spinosa) — elicits immediate rejection; and anyone who experienced these distasteful tastes knows that the tactile sensation follows, but after a short delay, the particular tannic taste.

Present-day primate species live in a taste environment where tannins may be prominent (Simmen et al., 1999a). Behavioral adaptations to minimize the anti-nutrient action of tannins, resulting from their strong tendency to bind with

proteins, have been described in nonhuman primates. The observation that Colobus monkeys (Procolobus kirkii) eat pieces of charcoal when food plants have a high content of condensed tannins has been explained by the adsorbent property of charcoal, preventing tannins to bind with proteins (Struhsaker et al., 1997). Clay can be eaten by primates in small amounts to achieve the same end (Hladik and Gueguen, 1974; Johns, 1990; Mahaney et al., 1996). Besides, tolerance of noxious compounds through behavioral adaptations may reflect the possible beneficent effects of some bitter or astringent compounds, and thus be adaptive. As an example, we can mention the utilization of bitter and related constituent of Vernonia amygdalina by chimpanzees during sickness (Huffman and Seifu, 1989); this response was probably determined by conditioning.

Such conditioned preferences and/or aversions should also have determined food choices and preferences in early hominids. Modern humans have developed techniques to eliminate, in food plants, most tannins and other "secondary compounds" such as saponins, terpenes, and alkaloids (Johns, 1990). This is why most of the bitter or tannic tastes have been almost entirely forgotten in modern civilizations. However, the evolutionary trend favoring the avoidance of anti-nutrient or toxic compounds still characterizes the human taste system. The relationship that we found between tannins and quinine tasting (Fig. 1) is an indirect evidence of the adaptation to cope with noxious substances, a characteristic of all primate species.

Concluding remarks: evolutionary trends

vs. environmentally learned (cultural) human taste responses

Although food preferences and food choices can rapidly adapt to changes of composition through conditioning, the gustatory system of each primate species has physiological, genetically determined, characteristics allowing initial adaptive responses to food composition (Hladik and Simmen, 1996). However, taste perception —the target of selective pressures— is not a simple relationship between a “basic taste quality” and a peripheral receptor. Since transduction mechanisms are not totally elucidated, we can suggest a simplified representation of a peripheral taste signal with several types of receptors simultaneously flashing. Partly similar sets of receptors would be flashing for partly similar tastes (i.e tastes of sugars, or the various “bitter” tastes). Conversely, the absence of collinearity observed when comparing the thresholds for some substances (i.e. sugars, as opposed to quinine/tannins) would reflect large differences in the sets of receptors flashing simultaneously. This complex coding system, with its polygenic determination, is not a simple target for selective pressures.

As a result, sensitivity to substances currently used in taste studies, such as salts and acids, is not clearly associated with evolutionary processes. Arguments against the very existence of a primary taste shaping for these compounds, are: (1) In man,

there is no evidence of a genetic determination of taste sensitivity to sodium chloride and citric acid (Krondl et al., 1983). (2) With the human data at hand, no clear aggregative pattern was found between thresholds for sodium chloride and clearly identified clusters (Figure 1), despite a weak tendency to cluster with citric acid perception and the quinine/tannins group. (3) Concerning nonhuman primates, isolated taste fibers responding best to sodium chloride (or other salts) and to citric acid (or other acids) were identified by Hellekant et al. (1997b); however their specificity can be low (these fibers also convey signals for other compounds) and varies across species. (4) The low sodium chloride content of natural primate foods is below threshold (although covering mineral requirements in diets; see above).

In this context, what is saltiness perception and what led to the present status of salt in human foods? Sodium chloride presently appears as an essential element in food composition and taste. In human groups, the hedonic response to salty solutions, up to medium concentrations, is generally pleasantness (Beauchamp et al., 1991). But it can be strong aversion, as among the Inuit inhabiting the icy coastal fringe of Greenland (Robbe and Hladik, 1994). This ambiguous responsiveness is not necessarily based on genetics and adaptation, although a possible recent selective trend towards high salt sensitivity has been discussed by Hladik and Simmen (1993).

Since adding sodium chloride can mask a bad taste and improve food flavor (Stevens, 1996), salt very likely became a precious object of exchange during human beginning, as food processing was being developed. One can wonder how and when coastal salt deposits have been first exploited and traded by hominids. Could it have occurred during the Pleistocene, as early as when stone flakes were being carried over long distances, as shown by paleontological evidence (Goebel, 1999)?

We must keep in mind that sociocultural traits are certainly the most important factors influencing perception and feeding behavior (Rozin, 1990; Garine, 1997). In any case, the gustatory system may be redundant with other systems in the detection of adequate foodstuffs. In the context of food consumption, a taste complex signal may rarely correspond to the responses observed when using solutions of purified compounds to determine taste thresholds. Integration of the taste signal and learned responses mediates food perception, preferences and choices, through a neural network in which taste pathways are interconnected with olfactory and visual pathways (Rolls, 1997). Touch is also concerned, and the trigeminal system may also determine strong stimulations, up to producing painful responses with strong acids, alcohol, or hot pepper.

Taste categorization may also result from cultural exposure. As Faurion (1993) stated, limitation of semantics in western languages originated the long standing theory of the "basic tastes". Cross-cultural studies are necessary in order to avoid the reductionism of having four "basic tastes" (sweet, bitter, salty and sour) that correspond to four words in western languages, with just a fifth taste, umami, recently imported from the Japanese. For instance, the Baka Pygmies in Cameroon use the same word for salty and sweet (Hladik, 1996), within a cultural environment

valorizing such perceptions (Hladik and Bahuchet, 1994). In Rajasthan, a quite different environmental and cultural context, two different words apply to tannin tastes —one for "good tannin" and one for "bad tannin"— (Françoise Cousin, personal communication). Similarly, in Yakutia, the eldest persons used to drink a decoction of oak bark were not only able to name it, but to discriminate this peculiar taste out of the two tannins during the blind tests (Malet et al., 1999). Finally, various descriptions of tannin tastes, also observed by Iaconelli (2000) among people of Southern Europe, are classical subjective perceptions among wine drinkers and beer amateurs.

Going back to an evolutionary perspective: taste can be viewed as the result of selective pressures linked to nutrient content and toxicity of potential foods, but operating exclusively within a two-directions system, instead of the system of four or more discrete basic entities.

Acknowledgements

Most research funds have been provided by the respective Institutions of the authors (Muséum National d'Histoire Naturelle and CNRS). Funds from the European Union (DG V-SOC 97 200420 05F02, M. Gerber and M. Padilla, coord.) allowed to carry out part of this research in Italy, Spain, France, Belgium and UK. Finally, many thanks are due to S. Ulijaszek (Oxford University) and to O.F. Linares (Smithsonian Institution) for their comprehensive comments and suggestions to improve the first version of our text.

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	N	Mean threshold	Threshold (log)	SD	95% fiducial limits
SUCROSE		(mM/l)			
	412	**13.31**	**1.12**	**0.38**	**1.10-1.15**
FRUCTOSE		(mM/l)			
	406	**26.18**	**1.42**	**0.43**	**1.36-1.48**
Sodium chloride	**407**	(mM/l) **12.46**	**1.10**	**0.49**	**1.05-1.16**
QUININE hydrochloride	**373**	(µM/l) **12.25**	**1.08**	**0.62**	**1.03-1.14**
citric acid		(mM/l)			
	399	**1.72**	**0.23**	**0.41**	**0.17-0.30**
tannic acid		(µM/l)			
	330	**156.77**	**2.20**	**0.64**	**2.15-2.24**
oak tannin		(mg/l)			
	335	**335.15**	**2.52**	**0.57**	**2.47-2.59**

Table 1 . Mean recognition taste thresholds calculated by probit analysis for all tested human adults from various populations.

	Sucrose	Fructose	Sodium	Quinine	Citric	Tannic	Oak	PROP
			chloride	hydrochl.	acid	acid	tannin	status
SUCROSE	**1.00**	**0.51****	**0.11***	**0.08**	**0.02**	**-0.01**	**0.01**	**0.05**
		N=407	*N=407*	*N=373*	*N=399*	*N=330*	*N=334*	*N=326*
FRUCTOSE		**1.00**	**0.14****	**0.10**	**0.03**	**-0.07**	**0.11**	**0.09**
			N=402	*N=368*	*N=394*	*N=326*	*N=330*	*N=322*
Sodium		**1.00**	**0.20****	**0.17****	**0.14***	**0.18****	**0.11***	
chloride				*N=369*	*N=395*	*N=330*	*N=333*	*N=322*
QUININE				**1.00**	**0.17****	**0.32****	**0.39****	**0.06**
hydrochloride				*N=363*	*N=326*	*N=331*	*N=316*	
citric acid					**1.00**	**0.24****	**0.18****	**0.04**
						N=327		

	N=330	*N=315*	
tannic acid			**1.00**
	0.50**	**0.01**	
	N=321	*N=278*	
oak tannin			
	1.00	**0.04**	
		N=282	

* p<0.05 **p<0.01

Table 2 . Pairwise Pearson correlation matrix of taste thresholds (log), including PROP sensitivity (taster vs. non taster).

Figure 1 . Cluster tree of taste thresholds for various substances (average linkage method) for all tested human adults (N=412).